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INTERACTION BETWEEN MORPHOLOGY AND HABITAT USE: A LARGE-SCALE APPROACH IN TROPIDURINAE LIZARDS

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Abstract. Habitat use can be used to predict morphological proportions among lizard species, building links between form and function. Among the Tropidurinae, a species-rich clade of lizards, these ecomorphological relations have not been studied for all the genera, and previous work still leaves some important gaps within this topic. In this study, a large-scale ecomorphological assessment of 10 genera found within this clade was performed with respect to habitat use categories. The results of a multivariate analysis that considered 14 morphological traits showed that *Stenocercus* was the most morphologically diverse genus within this clade. *Tropidurus* was the genus that showed a greater diversity of specialized species regarding habitat use, showing representative species for each category and the respective specialized morphologies; however, this apparent diversity was limited in general terms and appeared to be restrained by evolutionary history. Further analyses in a phylogenetic context showed that the effect of habitat use was not strong enough to explain the morphological diversity of the Tropidurinae. Finally, a phylogenetic signal test showed that all individual traits were dependent on evolutionary history; additionally, the limb traits exhibited a stronger phylogenetic influence than the rest of the traits. The Tropidurinae were found to be a morphologically diverse group of lizards where the influence of habitat use on the morphology seems to be constrained by specific morphological limits imposed by the evolutionary history of each genus. Further studies are needed to assess the effect of habitat use in the morphology within each separate genus of this clade, especially for those for which information is scarce.

Key words: adaptive radiation; diversity; ecomorphology; evolutionary history; *Stenocercus*; *Tropidurus*

INTRODUCTION

Adaptive evolution allows populations to increase their performance with respect to the surrounding environment through the evolution of beneficial traits that increase fitness. Some of the most obvious traits that can be shaped as a result of this process are the morphological characteristics of an organism. The ease of study of these traits has led to decades of research that has demonstrated strong links between morphology and ecology (Pianka, 1973; Arnold, 1983; Aerts et al., 2000). Several of these studies have linked morphological traits of

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Table 1. Relationship between morphological traits and ecological functions reported in past studies.

Trait	Function	Reference
Head shape	diet, foraging mode, antagonistic interactions	Herrel et al., 2001a,b, 2008; Vidal et al., 2006; McBrayer and Corbin, 2007
Forelimb length	maneuverability, escape behavior	Jaksic and Núñez, 1979; Vanhooydonck et al., 2000; Knox et al., 2001
Hind limb length	sprint speed, jump performance, habitat use	Losos, 1990; Losos et al., 1997, 1999; Aerts et al., 2000, Vanhooydonck et al., 2000; Kohlsdorf et al., 2001
Body shape	habitat use	Melville and Swain, 2000; Goodman and Isaac, 2008
Toes	habitat use	Miles, 1994; Zani, 2000; Grizante et al. 2010

different taxa to ecological characteristics, considering these relationships to be a product of natural selection (Collette, 1961; Carrascal et al., 1990; Winemiller, 1991; Aguirre et al., 2002).

Many different types of organisms have been studied with respect to ecomorphological traits. Among them, lizards are considered to be an important model system because of their relatively fast evolution, especially in terms of ecomorphological associations (Losos et al., 1997, 1999; Vitt et al., 1997a; Herrel et al., 2001c, 2008). The study of lizards in an ecomorphological framework has revealed strong links between ecology, performance, and morphology (e.g., Losos, 1990; Vitt et al., 1997a, Vanhooydonck et al., 2000; Perry, 2007), showing repeated patterns that allow us to predict the shape and design of an organism with respect to its environment and vice versa (Table 1).

Various ecological characteristics like diet, antagonistic interactions, and even reproduction can affect the morphology of lizards. Among these ecological characteristics, habitat use has been demonstrated to be a very influential factor in morphological diversification (Bickel and Losos, 2002; Elstrott and Irschick, 2004; Goodman et al., 2008). The results of several studies allow us to link species' habitats with specific shapes that seem beneficial in a given environment. Consequently, it is possible to predict how certain morphological traits are shaped in response to the habitat preference of the species.

The Tropidurinae are a group of iguanid lizards that can be divided into three subclades following Schulte et al. (2003): Tropidurini, Liolaemini, and the genus *Leiocephalus*. The Tropidurinae are generally considered to include 12 genera: *Ctenoblepharys*, *Eurolophosaurus*, *Leiocephalus*, *Liolaemus*, *Microlophus*, *Phymaturus*, *Plica*, *Stenocercus*, *Strobilurus*, *Tropidurus*, *Uracentron*, and *Uranoscodon*, which have diversified across South America (and the Caribbean in the case of *Leiocephalus*) through a process of adaptive radiation. This diversification has allowed them to occupy different habitats and environments, from tropical rain forests to deserts and dry forests (Zug et al., 2001). The diversity of habitats occupied has promoted the evolution of different strategies in terms of morphology and behavior, consequently triggering a high diversity in forms and performance (Pianka and Vitt, 2003).

Across the years these numerous relationships among ecology, morphology, and behavior have been studied within some of the genera in this group (Kohlsdorf et al., 2001, 2004; Schulte et al., 2004; Gifford et al., 2008; Toyama, 2016) and occasionally on a larger scale considering more than one genus at once (Kohlsdorf et al., 2008; Grizante et al., 2010, Tulli et al. 2009, 2016). However, information is lacking for some genera regarding ecomorphological patterns. With respect to the ecological characteristics of the species from this group, available information is relatively abundant, but still incomplete (Frost and Etheridge, 1989; Frost, 1992; Vitt and Zani, 1996; Vitt et al., 1997b; Ellinger et al., 2001; Pérez and Balta, 2007; Nogueira and Rodrigues, 2006, among several others). This is probably because the vast number of species in the Tropidurinae makes it difficult to have a complete data set, subsequently limiting the possibility of performing ecomorphological studies.

As mentioned above, tropidurine lizards use a great variety of different habitats. The genera *Uracentron*, *Uranoscodon*, and *Plica* contain species that are mainly arboreal (Howland et al., 1990; Vitt and Zani, 1996; Vitt et al., 1997b; Ellinger et al., 2001); *Phymaturus* species present strikingly flat bodies and heads, probably linked to their occupation of rocky habitats (Abdala and Quinteros, 2013). Most *Stenocercus* species diversified in the Andes (Cadle, 1991; Torres-Carvajal, 2007a,b), where the altitudinal gradients have triggered adaptive radiations in other taxa. *Tropidurus* are distributed mainly in open areas on the eastern side of the Andes and in the Amazon rain forest (Carvalho et al., 2013); *Microlophus* species are distributed in arid zones from northern Chile, passing through the Peruvian coast, to southern Ecuador (Dixon and Wright, 1975), and including the Galapagos Islands (Benavides et al., 2009). *Liolaemus* species inhabit the southern part of the continent, covering mostly arid habitats (Abdala and Quinteros, 2013). *Leiocephalus* is the only genus of this group that can be found outside South America, its main distribution being in the Caribbean Islands (Etheridge, 1966). Finally *Ctenoblepharys* is a monospecific genus that is the sister taxon of *Liolaemus*, sharing the same preference for arid environments (Abdala and Quinteros, 2013).

Given this diversity, several hypotheses can be constructed with respect to ecomorphological associations of the genera in this group. However, even though most of the genera primarily occupy a particular habitat, it is not uncommon to find species with different habitat preferences within the same genus. The relation between morphology and these distinct habitats has been studied before on a large scale within some tropidurine genera, showing contrasting results (Jaksic et al., 1980; Vitt et al., 1997a). Moreover, as overlap between habitat types and genera is common, the influence of evolutionary history must be considered. Phylogenetically, tropidurine genera have been widely studied and phylogenetic hypotheses are available for most of them (Schulte et al., 2000; Frost et al., 2001; Benavides et al., 2007; Torres-Carvajal, 2007b; Morando et al., 2013; Pyron et al., 2013), allowing associations between morphology and ecology to be analyzed in a phylogenetic context.

This diversity offers an opportunity to evaluate how morphological evolution occurs in the context of the occupation of several different types of habitat, allowing this study to test the previously found patterns on a larger scale. In that context, this study seeks to answer the following questions:

1. How are the Tropidurinae morphologically organized? Which are the exceptionally diverse genera in terms of morphology?
2. What is the influence of habitat use on the morphological traits of this group? Which

are the exceptionally diverse genera in terms of morphology related to habitat use?
3. How strong is the influence of habitat use on morphological diversity?
4. Is there an influence of evolutionary history on morphology within this group?

METHODS

Morphological measurements were taken on 1,048 specimens of 154 different species representing 10 of the 12 genera within the Tropidurinae: *Ctenoblepharys, Leiocephalus, Liolaemus, Microlophus, Phymaturus, Plica, Stenocercus, Tropidurus, Uracentron*, and *Uranoscodon*. Between 2 and 31 specimens were measured for each species according to availability. These specimens were obtained from the Museum of Comparative Zoology (MCZ) of Harvard University (Supplemental Table 1[1]). Fifteen morphological traits were considered in the analysis: snout–vent length (SVL), head length, head width, head height, body width, body height, distance between limbs, femur, tibia, metatarsus, longest toe of the hind limb, humerus, radius, metacarpus, and longest toe of the front limb. As most specimens' tails were incomplete, regenerated, or damaged, only including specimens with intact tails would have significantly lowered the sample size, so this trait was not considered. All measurements were manually taken with a digital caliper (precision 0.01 mm) by the author.

Habitat use data for each species were gathered from the existing literature (Supplemental Table 2), considering the type of ecosystem or behavior as an indicator of this variable when the information was not clear or specific. Given the great diversity in ecology and behavior found in this clade, it would be highly difficult to precisely categorize all the studied species regarding their habitat preferences, so four habitat use categories were assigned: arboreal, ground dweller, rock dweller, and sand dweller. In many cases this information could not be found, reducing the number of species used for habitat use analysis to 117. When a given species was categorized as a generalist or found to occupy different habitat types, it was associated with the habitat in which it has been more commonly reported on the basis of published information.

The phylogenetic reconstruction was based on the previously built squamate phylogenetic tree constructed by Pyron et al. (2013) where 12,896 base pairs from seven nuclear loci (BDNF, c-mos, NT3, PDC, R35, RAG-1, and RAG-2) and five mitochondrial genes (12S, 16S, cytochrome *b*, ND2, and ND4) were used. The original tree was trimmed to match the species of this study for which habitat use information was available, leaving 94 species in the final phylogeny (Fig. 1). Additionally, an extra tree was constructed using all the matching species between this work and the study of Pyron et al. (2013) without considering the availability of habitat use information. This second tree included 111 species and was used for posterior phylogenetic signal analyses (see below).

Analysis. The 14 morphological variables were regressed against SVL and residuals were averaged for each species. A principal component analysis (PCA, covariance matrix) was performed using these averages of each trait for each species to reduce the number of variables used in the posterior analyses. The first PCs, which together explained more than 85% of the total variation, were then retained to calculate the Euclidean distances between every pair of species within each genus (except *Ctenoblepharys*, *Plica*, *Uracentron*, and *Uranosco-*

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[1] Supplemental material referenced in this paper is available online at www.mcz.harvard.edu/Publications/.

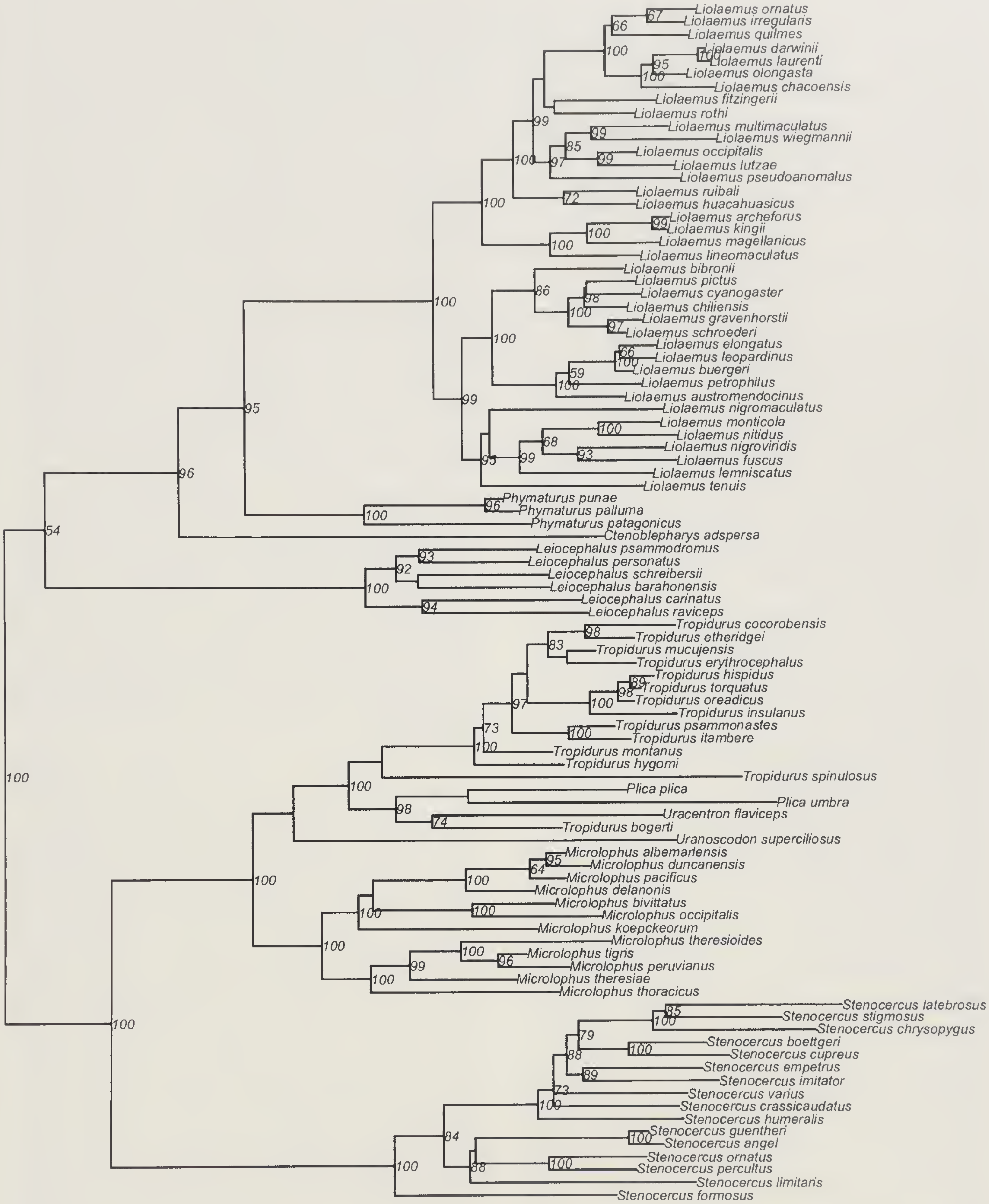

Figure 1. Phylogenetic tree (94 species) utilized for the phylogenetic analysis. Branch lengths are proportional to expected substitutions per site. Numbers at nodes are branch support values greater than 50%. Obtained and modified from Pyron et al., 2013.

don, which are represented by only one or two species in this study). The scores of each component were scaled to reflect the proportional differences between their eigenvalues; these transformed scores were later used to calculate the Euclidean distances following the formula:

$$D_{ij} = \left[\sum_{k=1}^{y} (X_{ik} - X_{jk})^2 \right]^{\frac{1}{2}}$$

where D_{ij} is the Euclidean distance between species i and j, and X_{ik} and X_{jk} are the scaled scores of the PC k for species i and j. Euclidean distances were measured for every pair of species within a genus to reflect the morphological distinctiveness between them, so that longer distances represent bigger differences. Using these sets of Euclidean distances, the following variables were calculated for each genus following Ricklefs et al (1981): average nearest neighbor distance (NND), average farthest neighbor distance (FND), and the average distance. Average NND and FND for each genus were calculated averaging the distance values of the closest and farthest other species (on the basis of Euclidean distances) of each species of a given genus respectively. Average distance was the average of all the distances calculated between every pair of species. Within each genus, greater average values of these variables would mean a greater morphological diversity. Additionally, a simulation of how these variables would behave in random groups of species was performed. Various groups of different numbers of species chosen at random were created from the pool of analyzed species for neighbor distances, and NND, FND, and average distance were calculated for each of these simulated groups. The simulation for a given group size was repeated 100 times and the averages for the NND, FND, and average distance were calculated and used for comparison against the real data. The results of simulations of different size groups were used to represent the values of these variables that would be expected by chance.

A discriminant function analysis (DFA) was also performed on the 117 species for which habitat use information was available, categorizing them using the four defined habitat use groups. Euclidean distances were again calculated using the scores given by each function and scaling them depending on the percentage of variation explained by each function. New simulations and comparisons using groups of randomly chosen species were also performed following the same method as mentioned above. The DFA identifies which morphological traits are related to particular habitat use categories. Given that different morphologies are grouped with respect to habitat use categories, a genus whose species are relatively diverse in terms of habitat use preferences is expected to show values of Euclidean distances similar to the ones obtained by the simulations.

A multivariate analysis of variance (MANOVA) was performed in a phylogenetic context using the habitat use categories as the independent variables and the PCA scores from the first axes previously obtained as the dependent variables to confirm or deny the influence of habitat use on each of these morphological variables. This phylogenetic MANOVA was performed in R (R Core Team, 2016), using the "aov.phylo" function (1,000 simulations, Wilks' λ) from the Geiger package (Harmon et al., 2008). A phylogenetic ANOVA based on 1,000 simulations was performed with the function "phylANOVA" from the phytools package (Revell, 2012) as an a posteriori analysis to assess the differences between habitat use categories with respect to each PC. This analysis specifies which PCs are associated with habitat use and also indirectly indicates

Table 2. Loadings of the first five axes from the principal components analysis for each morphological variable.

Variable	PC1	PC2	PC3	PC4	PC5
Head length	−0.313	0.086	−0.266	0.304	−0.275
Head width	−0.120	−0.271	−0.639	0.135	0.060
Head height	−0.190	0.352	−0.443	−0.011	0.391
Body width	0.083	−0.481	−0.143	−0.452	−0.086
Body height	−0.121	0.345	−0.283	−0.440	0.268
Dist. limbs	0.194	−0.319	0.103	−0.194	0.642
Femur	−0.333	−0.126	0.058	−0.194	−0.100
Tibia	−0.377	−0.012	0.099	−0.229	−0.106
Metatarsus	−0.364	0.031	0.136	−0.317	−0.131
Hind toe	−0.326	0.260	0.342	−0.109	0.169
Humerus	−0.292	−0.295	0.038	−0.001	0.099
Radius	−0.323	−0.213	0.053	0.080	0.058
Metacarpus	−0.219	−0.341	−0.083	0.114	−0.012
Front toe	−0.251	−0.098	0.234	0.482	0.443

whether habitat use has a strong influence on the overall morphological diversity (this would be confirmed if habitat use influences the first PCs, which explain most of the morphological variation). An additional phylogenetic ANOVA was performed using the individual traits' residuals as dependent variables to assess the differences between habitat categories with respect to each individual trait.

Finally, phylogenetic signal was tested for each individual trait utilizing the second tree constructed as mentioned previously. The function "phylosig" from the phytools package (Revell, 2012) was used to measure Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) as indexes of phylogenetic signal. Theoretically, the K and λ statistics take values from 0 to infinity; values lower than 1 result when the phylogenetic signal for a trait is lower than that expected by a model of Brownian motion evolution, which means that closely related species resemble each other less than expected under this model for a given trait. A value higher than 1 means that closely related species are more similar to each other than expected by a model of Brownian motion evolution for a given trait. Significant differences between both statistics and values of zero (K or $\lambda = 0$) or one (K or $\lambda = 1$) were tested.

RESULTS

The five first axes of the PCA, which together explained about 87% of the total morphological variation, were retained for further analysis. The loadings for each PC are shown in the Table 2. A scatter plot defined by PC1 and PC2 showed that species were grouped mainly by genus (Fig. 2). PC1 explained 54.4% of the variation and was strongly related to all the limb traits' lengths and head length; PC2 explained 13.3% of the variation and was related to a contrast between all the front limb traits, body width, head width, and distance between limbs versus head height, body height, and hind limb toe. PC3 explained 9.2% of the variation and loaded for a contrast between head length, width, and height and also body height versus hind and front toes. PC4 explained 5.9% of the variation and loaded for a contrast between body width and height, and also for tibia and metatarsus (with weaker loadings for femur and distance

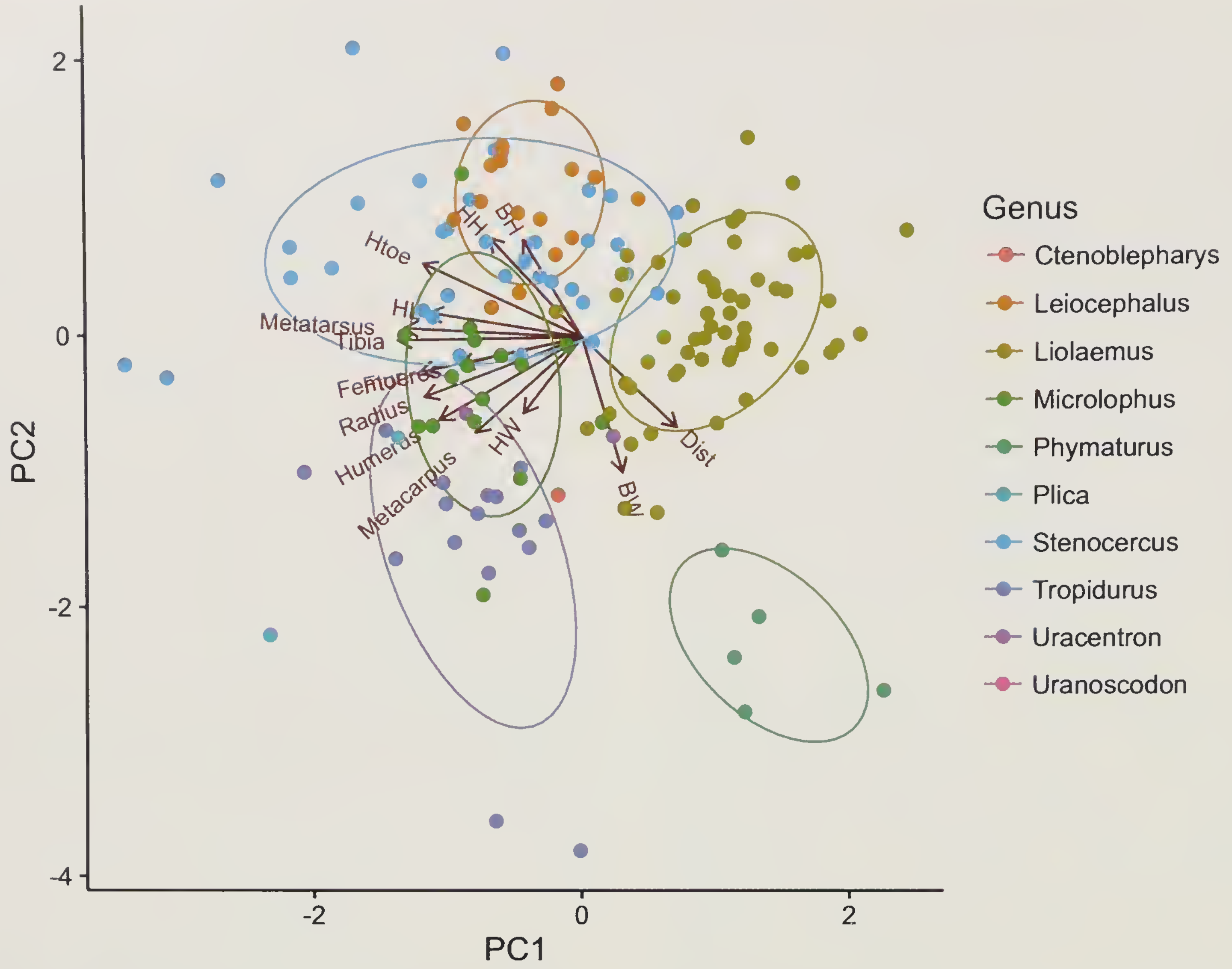

Figure 2. Scatter plot showing the morphological space defined by PC1 and PC2. Abbreviations are shown for some traits as HL (head length), HW (head width), HH (head height), BW (body width), BH (body height), Dist (distance between limbs), Htoe (longest toe of the hind limb), and Ftoe (longest toe of the forelimb).

between limbs) versus head length and front toe. Finally, PC5 explained 4.2% of the variation and loaded for a contrast between head length versus head height, distance between limbs, and front toe (Table 2).

Values of NND, FND, and average distance for each genus were compared against simulated values that produced the expected distances for randomly grouped species (Fig. 3 A, B, C). For the average NND (Fig. 3B), the values for all the genera analyzed were lower than the simulated ones, meaning that the species within each genus were morphologically more similar than expected by chance. For the average FND (Fig. 3A), the values for all the genera except *Stenocercus* were lower than the simulated ones. *Stenocercus*' value was significantly higher when compared with the other genera and was almost equal to the simulated one. The same pattern was observed for the average distances (Fig. 3C); all the genera except *Stenocercus* showed significantly lower values when compared with the simulated ones, whereas *Stenocercus* was not significantly different from the simulation value.

The DFA differentiated the species by habitat use category, with 75.2% of species assigned to the correct category; the scatter plot of DF1 and DF2 showed a clear differentiation between groups, especially between arboreal species and the rest of categories (Fig. 4). However, sand species were too similar to the ground ones to be

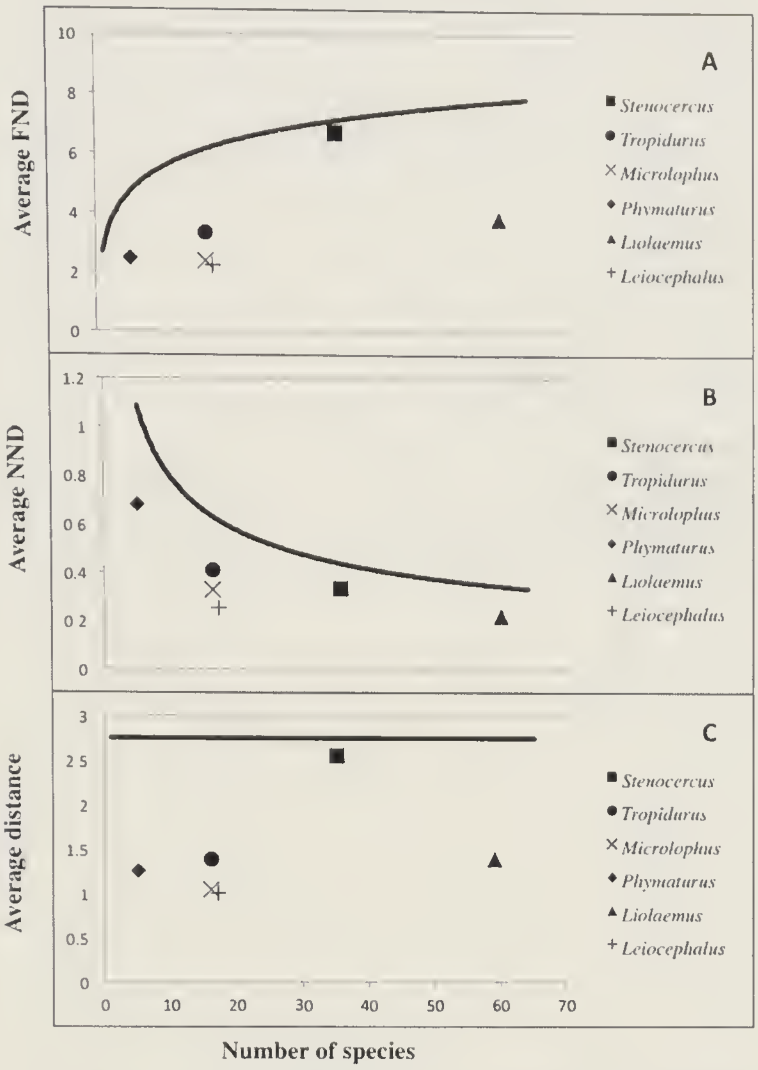

Figure 3. Comparison of average FND (A), NND (B), and average distance (C) between all the analyzed genera (symbols) and simulated groups of random species (solid black lines).

correctly classified using these functions; only 6 of 17 were correctly classified, whereas the other 11 were assigned to the ground (9) and rock (2) categories (results not shown). DF1, DF2, and DF3 explained 52.1, 40.3, and 7.6% of the total variation respectively. The DF1 loaded for a contrast between head width, body height, distance between limbs, femur, hind-limb toe, and radius versus head height, body width, tibia, and metatarsus. The DF2 loaded for a contrast between head height, body height, metatarsus, hind-limb toe, and humerus versus body width, femur, radius, and forelimb toe. Finally, DF3 loaded for a contrast between head length, body width, femur, hind-limb toe, and metacarpus versus head width, tibia, and metatarsus (Table 3). When comparing the average DF scores of different habitat use categories, arboreal species were found to be separated from the rest by DF1 (Fig. 5A), whereas DF2 separated arboreal and ground species from rock and sand dwellers (Fig. 5B). DF3 separated sand dwellers from the other categories (not shown).

As with the PCA scores, values of NND, FND, and average distance for each genus were compared against simulated values, this time using the scaled DF scores as the traits utilized to construct the Euclidean distances. For the average FND (Fig. 6A), the value for *Microlophus* was slightly lower than the simulated value, whereas the *Stenocercus* and *Tropidurus* values were almost the same as the respective simulated values. All the other genera values were significantly lower than the simulation ones. For the average NND (Fig. 6B), a similar scenario was observed: *Microlophus* showed a value that was lower than the simulated one, but still inside the confidence range. *Stenocercus* and *Tropidurus* again showed values that were similar to the simulated ones. The average distances (Fig. 6C) showed again the same pattern, *Microlophus* being moderately lower than its respective simulated value, and *Stenocercus* and *Tropidurus* values being almost equal to the simulated ones.

The phylogenetic MANOVA indicated that there was a significant effect of habitat use in the PC scores of the species (df = 3, F = 5.54, Wilks' $\lambda = 0.437$, $P < 0.01$), but the phylogenetic ANOVA showed that only PC4 and PC5 scores were influenced by habitat use (PC4: F = 6.814, $P = 0.034$; PC5: F = 7.533, $P = 0.026$; Table 4). With respect to PC4, a significant difference was found between arboreal and ground categories ($t = 3.683$, $P = 0.040$), and between arboreal and sand categories ($t = 3.953$, $P = 0.012$). For PC5, significant differences were found between arboreal and ground ($t = 3.945$, $P =$

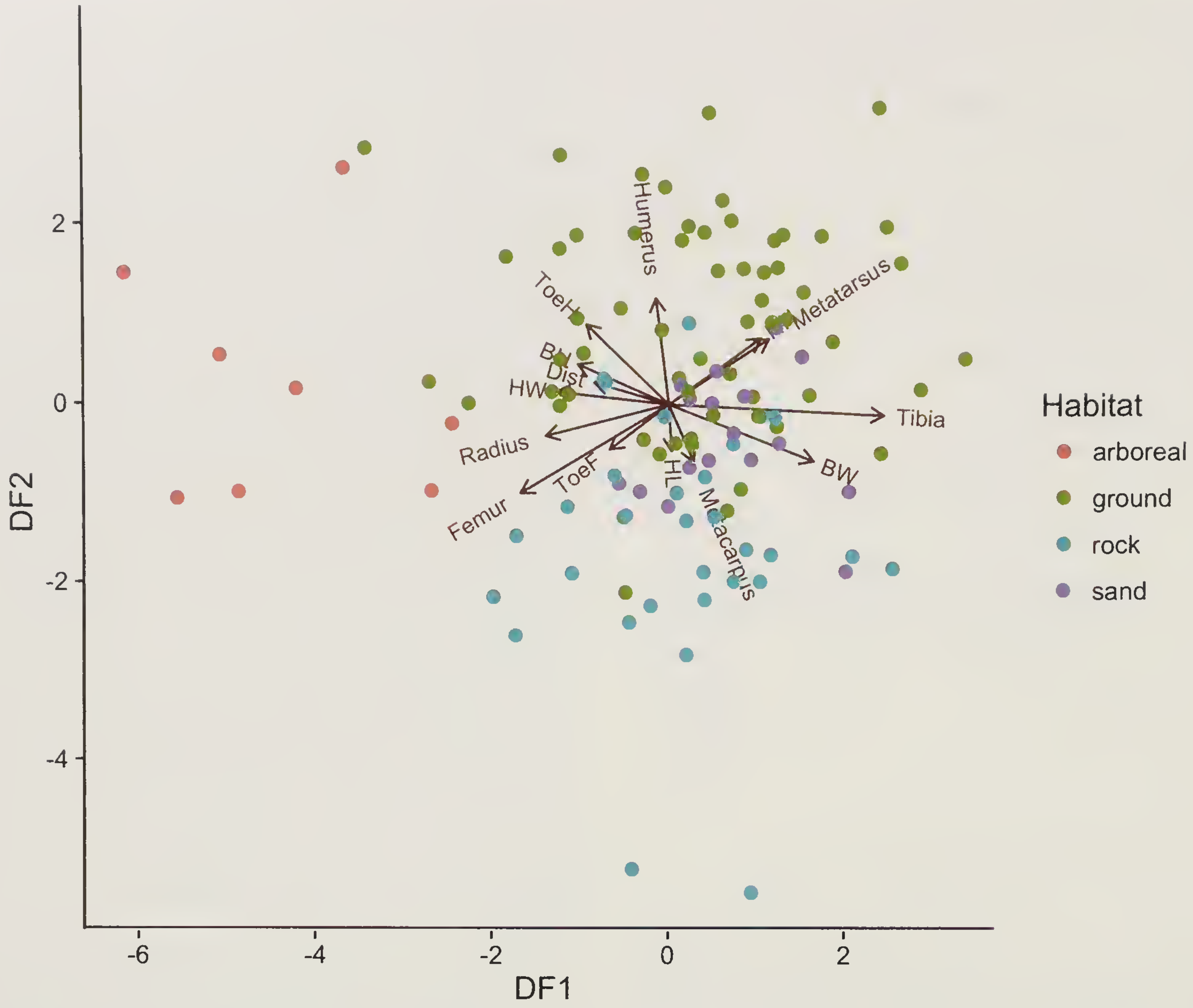

Figure 4. Scatter plot showing the morphological space defined by DF1 and DF2. Abbreviations of the traits are the same as shown in Figure 2.

0.048), arboreal and rock (t = 4.550, P = 0.006), and arboreal and sand categories (t = 4.294, P = 0.01).

The phylogenetic ANOVA with individual traits as dependent variables showed that only the longest toe of the forelimbs was influenced by habitat use (F = 8.265, P = 0.011). For this trait, significant differences were found between arboreal and ground (t = 4.076, P = 0.040), arboreal and sand (t = 4.966, P = 0.006), and arboreal and rock categories (t = 3.933, P = 0.025). The longest toe of the hind limbs and the body width showed a marginally significant association with habitat use (longest toe of hind limb: F = 5.590, P = 0.062; body width: F = 6.141, P = 0.073).

TABLE 3. LOADINGS OF THE THREE DISCRIMINANT FUNCTIONS OBTAINED WHEN PERFORMING A DFA USING HABITAT USE AS CATEGORY.

Variable	DF1	DF2	DF3
Head length	0.025	−0.428	−0.317
Head width	−0.943	0.115	0.943
Head height	0.767	0.605	0.048
Body width	1.214	−0.523	−0.339
Body height	−0.761	0.368	0.484
Dist. limbs.	−0.623	0.201	0.556
Femur	−1.240	−0.816	−0.810
Tibia	1.801	−0.104	0.620
Metatarsus	0.835	0.599	0.188
Hind toe	−0.691	0.732	−0.556
Humerus	−0.110	0.971	−0.017
Radius	−1.029	−0.289	1.260
Metacarpus	0.209	−0.525	−0.561
Front toe	−0.493	−0.412	−0.665

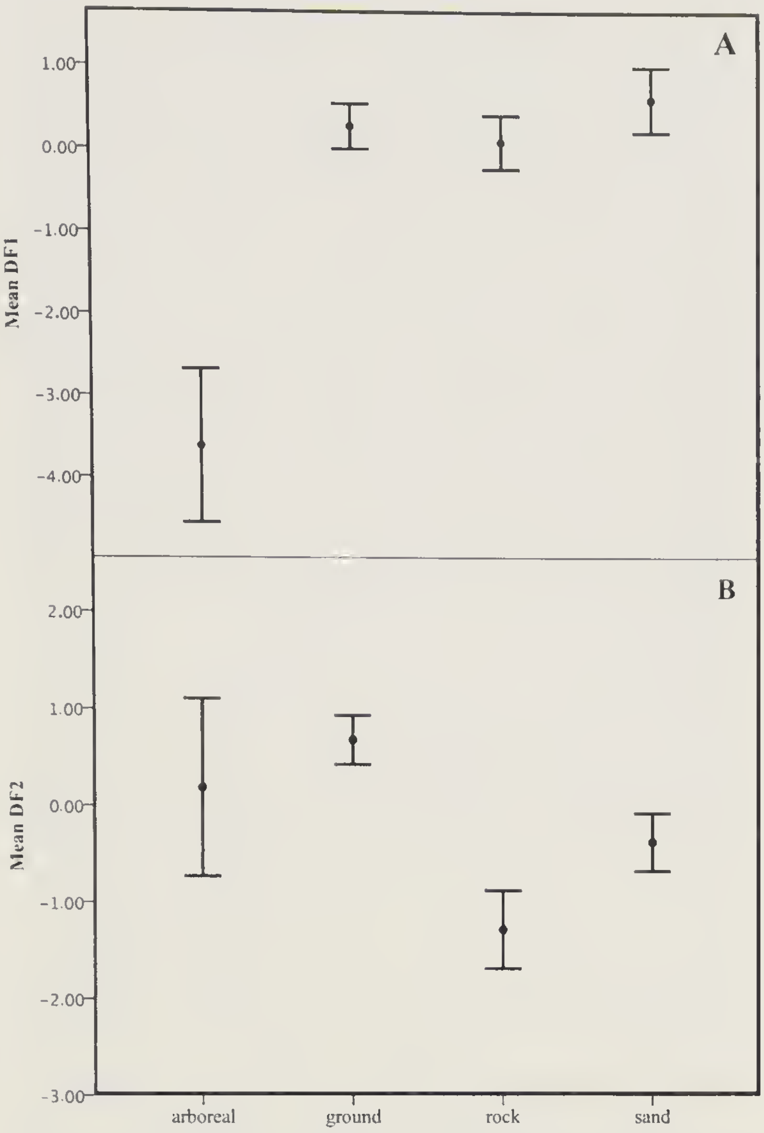

Figure 5. Comparison between habitat use categories between DF1 scores (A) and DF2 scores (B). Error bars represent 95% confidence limits.

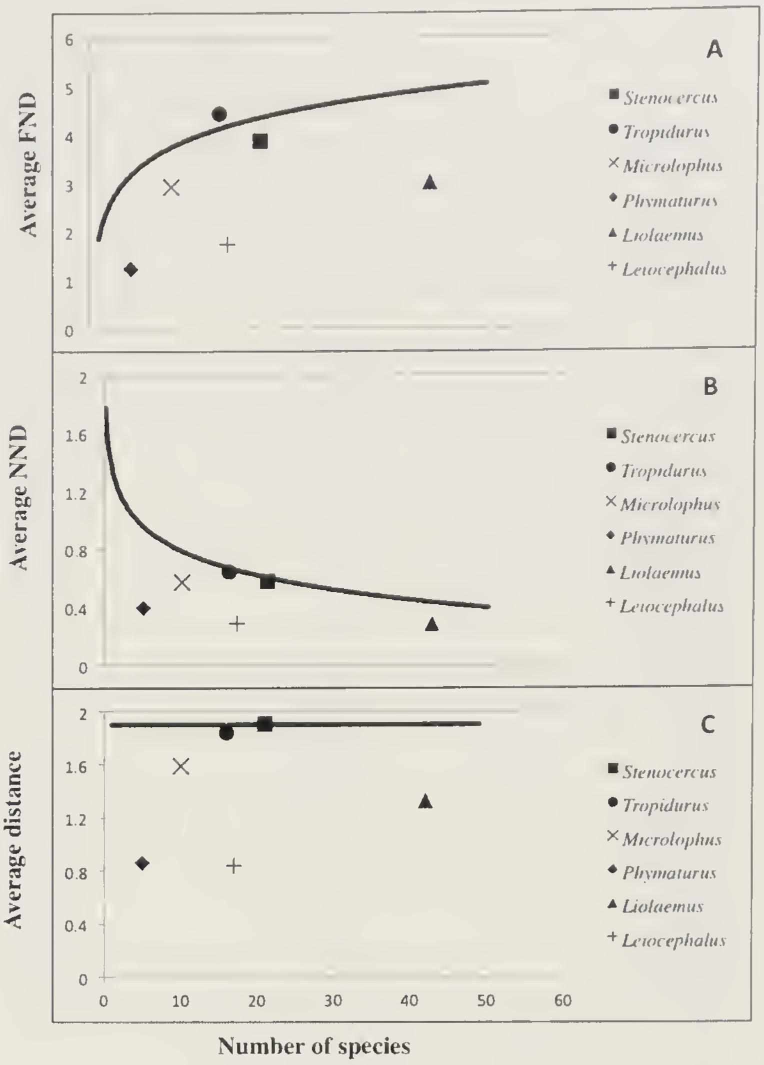

Figure 6. Comparison of average FND (A), NND (B), and average distance (C) between all the analyzed genera (symbols) and simulated groups of random species (solid black lines) using scores from the discriminant function analysis as traits.

All the traits were examined for phylogenetic signal using Blomberg's K and Pagel's λ statistics (see Methods). The results showed that all the traits were influenced to varying degrees by phylogeny, as all showed values of K and λ significantly greater than zero (Table 5). All the values of λ were also significantly lower than the expected under a Brownian model of evolution ($\lambda = 1$). The values of K for the femur, tibia, metatarsus, longest toe of the hind limb, humerus, and radius were not significantly different from those expected under a Brownian model of evolution ($K = 1$). The remaining were significantly lower (Table 5). In general, traits related to limbs showed stronger phylogenetic signals than other traits in both methods.

DISCUSSION

Does Evolutionary History Influence Morphology within the Tropidurinae? This study indicates that all the morphological traits of tropidurine species are influenced by phylogenetic signal (Table 5). This result is similar to what has been found for other groups of lizards, like gymnophthalmids (Barros et al., 2011). However, it contradicts the results of another study that examined tropidurids (Kohlsdorf et al., 2008), which found no evidence of phylogenetic signal on head traits. The use of a different phylogeny might have been responsible for these differences, as well as the different scale of both studies (this work comprising a larger number of taxa). However, the apparent

Table 4. Influence of habitat use on PCA scores and individual traits' residuals obtained from the phylogenetic ANOVA (see text for specific differences between categories). Significant results ($P < 0.05$) are shown in bold.

Variable	F	P
PC1	2.004	0.436
PC2	6.399	0.061
PC3	2.448	0.356
PC4	**6.814**	**0.034**
PC5	**7.533**	**0.026**
Head length	0.225	0.967
Head width	4.188	0.159
Head height	4.093	0.166
Body width	6.141	0.073
Body height	4.664	0.131
Dist. limbs	0.921	0.731
Femur	2.059	0.436
Tibia	0.891	0.769
Metatarsus	1.806	0.515
Hind toe	5.590	0.062
Humerus	3.018	0.292
Radius	2.811	0.297
Metacarpus	1.351	0.625
Front toe	**8.265**	**0.011**

lability of the head morphology found by Kohlsdorf et al. (2008) might support the results of this study given that head traits presented a lower phylogenetic signal than limb traits (Table 5). The results from both methods (Blomberg's K and Pagel's λ) showed that the phylogenetic signal was always significantly greater than zero; moreover, Blomberg's K was not different from the value expected under a model of Brownian evolution ($K = 1$) for the femur, tibia, metatarsus, longest toe of the hind limb, humerus, and radius (Table 5). This result suggests that these traits are strongly influenced by evolutionary history, following a trend of Brownian evolution dependent only on time and with little effect of natural selection.

How Strong Is the Influence of Habitat Use on the Morphological Diversity of Tropidurinae? The results of both MANOVA and ANOVA in a phylogenetic context revealed a small influence of habitat use on the evolution of the morphological traits of the studied species (Table 4). This influence was significant only on PC4 and PC5, demonstrating a weak influence of habitat use on morphological diversity as these two PCs explained only around 10% of the total morphological variation. The phylogenetic ANOVA on individual traits indicated that

Table 5. Phylogenetic signal for all the traits analyzed calculated with Blomberg's K and Pagel's λ. Significant P-values (in bold) correspond to the departure of the statistic from zero (P_0) or one (P_1).

	Blomberg's K			Pagel's λ		
Variable	K	P_0	P_1	λ	P_0	P_1
Head length	0.430	**0.001**	**0.038**	0.714	**<0.001**	**<0.001**
Head width	0.261	**0.001**	**0.001**	0.587	**<0.001**	**<0.001**
Head height	0.347	**0.001**	**0.014**	0.771	**<0.001**	**<0.001**
Body width	0.210	**0.019**	**0.001**	0.741	**<0.001**	**<0.001**
Body height	0.227	**0.006**	**0.002**	0.664	**<0.001**	**<0.001**
Dist. limbs	0.257	**0.001**	**0.005**	0.507	**<0.001**	**<0.001**
Femur	0.542	**0.001**	0.185	0.714	**<0.001**	**<0.001**
Tibia	0.740	**0.001**	0.531	0.937	**<0.001**	**0.017**
Metatarsus	0.565	**0.001**	0.247	0.765	**<0.001**	**0.011**
Hind toe	0.500	**0.001**	0.137	0.835	**<0.001**	**<0.001**
Humerus	0.437	**0.001**	0.067	0.638	**<0.001**	**<0.001**
Radius	0.830	**0.001**	0.724	0.924	**<0.001**	**0.002**
Metacarpus	0.393	**0.001**	**0.030**	0.626	**<0.001**	**<0.001**
Front toe	0.420	**0.001**	**0.036**	0.815	**<0.001**	**<0.001**

only one (the longest toe of the forelimb) of the 14 traits showed differences with respect to habitat usage. Specifically, arboreal species were separated from the remaining categories on the basis of PC4, PC5, and longest toe of the forelimb. This finding supports previous studies that have shown the positive association between toe length and claw morphology with an arboreal lifestyle (Ribas et al., 2004; Tulli et al., 2009). The results of both ANOVAs suggest that arboreal habits imply an important evolutionary change in morphology and point to arboreal lizards as the most specialized in terms of shape within this clade. However, this link between morphology and habitat use would not be the main cause of the morphological diversity within Tropidurinae.

What Is the Influence of Habitat Use in the Morphological Traits of This Group? Despite the relatively weak influence the different habitat use categories had on morphological diversity, the DFA showed some correlations between these categories and particular morphological traits. Arboreal species were easy to discriminate from the remaining species using the first discriminant axis and were characterized by possessing relatively longer forelimbs and shorter hind limbs, as well as higher and narrower bodies, characteristics that are in agreement with previous studies (Sinervo and Losos, 1991; Kohlsdorf et al., 2001). DF 2 separated rock-dwelling species from the other categories. Rock dwellers showed low scores for this function, indicating that they possessed flat bodies and heads and also long hind limbs. Similar results have been also observed in other rock-dwelling lizards from other taxonomic groups (Revell et al., 2007). Finally, the third axis separated sand lizards from the others. Sand lizards scored high on this axis, which loaded positively for femur, tibia, and metatarsus, among other characteristics. These traits are also known to be related to locomotor performance in sandy substrates (Bonine and Garland, 1999). Altogether, these results indicate that the patterns observed in other taxonomic groups of lizards are also applicable to the Tropidurinae.

Which Are the Exceptionally Diverse Genera in Terms of Both Morphology Related to Habitat Use and Morphology in General Terms? The simulations performed using the DF scores showed that *Stenocercus*, *Tropidurus*, and *Microlophus* (to a lesser extent) were dispersed randomly in morphological space (Fig. 6), which means that these genera have representative species showing morphologies associated with different habitat uses. Given that *Tropidurus* is a genus whose species are rich in habitat use categories (Supporting Information 2), this was expected. *Tropidurus* has previously been shown to have diversified widely in morphology (Bergallo and Rocha, 1993; Vitt et al., 1997a; Kohlsdorf et al., 2001; Grizante et al., 2010), occupying different types of habitats. Even though past studies considered *Plica* and *Uracentron* species as part of *Tropidurus*, the present results in this study, in which those genera were excluded from *Tropidurus*, indicate that the ecomorphological diversity of *Tropidurus* is substantial. This genus, however, is not diverse in terms of general morphology as demonstrated by the distance comparisons in Figure 3. These results might have two implications. First, the general morphological diversity of *Tropidurus* does not appear to be strongly mediated by the diversity of habitat use categories. If habitat use were correlated with morphological diversity, then *Tropidurus* should have exhibited a higher value at least for FND and average distance when using PCA scores. This idea is supported by the ANOVA results, which showed no interaction between any of the first three

PCs and the habitat use categories, and indicated that most of the morphological variation was not related to this ecological characteristic. Second, the DFA showed that interactions between habitat use and morphology do exist, consequently triggering a certain degree of variation in morphology (Fig. 5). This variation might not be observable when evaluating morphological diversity as a whole (Fig. 2), but might be acting locally within each genus, as demonstrated by *Tropidurus*. This second affirmation would be supported by the degree of phylogenetic signal in the morphological traits. It is important to consider that even though phylogenetic signal was present in all the traits, its intensity in each case when using Pagel's λ method was lower than the one expected under a Brownian model of evolution ($\lambda = 1$) and lower than that expected under the same model when using Blomberg's K ($K = 1$) in 8 of 14 traits. This result indicates a certain effect of adaptive evolution on the evaluated traits (Table 5). To test this hypothesis and to measure the effect of habitat use on a genus level, similar studies must be performed on a smaller scale, especially for the genera for which these studies are scarce.

Even though *Stenocercus* also showed average distances similar to those expected by chance when using DF scores (Fig. 6), this diversity cannot be associated with the evolution of different habitat use strategies, given that *Stenocercus* species were considered ground dwellers (Supporting Information 2). However, *Stenocercus* was not only morphologically diverse when distances were calculated with DF scores, but also when they were calculated with the PCA scores (Fig. 3). Moreover, this was the only genus that showed a spacing between species similar to that expected by chance when using distances based on PC scores (Fig. 3A, C). This result shows that *Stenocercus*' morphological diversity is at least not driven by the habitat use categories considered in this study. Furthermore, this diversity was so important that it was probably influential when performing the analysis using DF scores to calculate distances between species, making *Stenocercus* appear as a diverse genus in a habitat use context (Fig. 6). Instead of habitat use, other characteristics not considered here might be influencing the apparent diversity shown by *Stenocercus*. Past studies in another tropidurine genus, *Liolaemus*, failed to find any relation between morphology and habitat use, but have found correlations between morphology and escape behavior (Jaksic and Núñez, 1979; Jaksic et al., 1980; Schulte et al., 2004; Pincheira-Donoso et al., 2009), demonstrating that different ecological factors can affect morphology in different taxa. Foraging mode might be another possible reason for morphological variation, especially because it affects both diet and movement (McBrayer and Corbin, 2007), thus influencing a wide range of morphological traits. Moreover, *Stenocercus* is a genus that has diversified in the Andes mountains (Torres-Carvajal, 2007b), where other taxa have also radiated, taking advantage of the numerous ecosystems produced by its pronounced altitudinal gradient (Monasterio and Sarmiento, 1991; Bleiweiss, 1998; Elias et al., 2009). The influence of this ecological gradient on lizard ecomorphology is unknown and might be triggering new interactions between form, function, and behavior. It is important to note that *Stenocercus* is divided into two subclades and that ecomorphology might have diversified in different ways in the different regions. Additionally, a different categorization of habitat use (e.g., different microhabitats) might be valid for *Stenocercus*, the one used in this study being unable to capture a hypothetical diversity in terms of habitats utilized.

Microlophus did not show a high morphological diversity in the PCA, but was relatively diverse in terms of relevant habitat use traits. *Microlophus* has been separated from *Tropidurus* (Frost, 1992) and both genera share similar generalized morphologies (Fig. 2). The difference in the habitat types these genera occupy (arid vs. savanna/rain forest) might have consequently caused this difference in morphological diversity, given that the complexity of habitats in eastern South America might offer more and new opportunities for diversification in comparison with arid environments in the western coast (Moritz et al., 2000). *Microlophus* is also phylogenetically close to *Stenocercus* (Frost, 1992; Pyron et al., 2013), which showed a remarkable morphological diversity in this study; however, as with *Tropidurus*, this time the Andes would be triggering a higher morphological diversity when compared with arid zones. It is also possible that *Microlophus* does not have any special characteristic that would make it more diverse when compared with *Leiocephalus*, *Liolaemus*, or *Phymaturus*. In that case, it is possible that the Galapagos *Microlophus* have increased their morphological diversity because the islands present different ecological pressures when compared with the mainland. Additionally, gene flow between insular and continental populations is presumably restricted, thus accelerating the production of diversity in various dimensions. A comparison between insular and mainland *Microlophus* populations must be done in ecological and morphological terms to test this hypothesis.

The results of this work revealed the patterns of morphological organization within this group of lizards, evaluated the role of habitat use in morphological diversification, and also identified the most diverse genera in terms of morphology. The influence of phylogenetic closeness was also considered and measured, revealing which traits were subjected to its influence and how it affected the observed morphological patterns. Morphological traits in this clade of lizards appear to be phylogenetically restrained; however, a correlation between these traits and habitat use was identified and might be the main cause of morphological variation between species of the same genus. Moreover, some genera within this clade (like *Microlophus* or *Stenocercus*) have undergone important geographical separation and dispersion, resulting in well-defined subclades that have endured totally different selection pressures in the past. For this reason, more studies on an evolutionary framework are needed on a generic level to complement the results of this study, especially for the genera for which the information is still poor. Results of the present and previous studies indicate that morphology is a reliable predictor of habitat use and vice versa. However, this study showed that the apparent association between morphology and habitat use is not enough to explain the great diversity of forms observed in this clade of lizards. Future studies must focus on other important ecological and behavioral characteristics (e.g., foraging mode, escape behavior) to complement the information offered by habitat use alone to better understand the morphological trends observed in the Tropidurinae and other diverse clades of lizards.

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